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DESCRIPTION OF THE COMBINED PROGNOSIS/ WESTERN SPRUCE BUDWORM MODEL

VERSION 3.0

by

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INTRODUCTION

CANUSA-West is revising the current version of the combined Stand Prognosis/Western Spruce Budworm Model. The models are being developed for use in forest and forest pest management and in the land management planning process. These models will provide a basis for making economic analyses using available optimization techniques as can be found in MUSYC, TIMBER RAM-MODEL II, and/or FORPLAN.

This paper is intended to provide modelers with a guide to the computer program's organization, possible functional relationships, and an index to the subject matter specialists who will provide data required to parameterize the model. It is also intended to be used by cooperating CANUSA-West scientists as a source of information, a description of how their work will be incorporated into the models. It precedes the revised model and thereby facilitates the process of reviewing the form and function of the new model. We anticipate frequent revisions.

The Stand Prognosis Model (PROGNOSIS) is a stand growth simulator with user defined options for management and harvesting. PROGNOSIS has gone through four major revisions over the past decade and contains features capable of simulation of a variety of stand management practices (e.g., fertilization, precommerical- and commercial-thinning, harvest, and regeneration prescriptions) as well as other western pest problems (Douglas-fir tussock moth, mountain pine beetle) and related management activities. PROGNOSIS is being used over an expanding area. CANUSA-West will also support the incorporation of the Western Spruce Budworm Model (BWMOD) for use by other stand projection models. A new model is being developed by scientists at the Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado. We hope that before the Program ends in 1983, this new system will be developed sufficiently for incorporation of the relevant budworm model components.

This document is meant to serve as an outline for the new version of BWMOD and the interfacing foliage and damage models. The model was originally produced during a workshop held January 28-February 1, 1980, sponsored by CANUSA-West, and facilitated by LGL Ecological Research Associates, Inc., of Bryan, Texas. The facilitators used the approach described by Holling (1978). The results of this workshop, version 1.0, are available as an unpublished report (McNamee et al., 1980). Version 2.0 of the model was developed by Peter McNamee, working for the University of Idaho on a CANUSA-West cooperative agreement. No written report, other than extensively annotated computer code, is available to document version 2.0. Copies are available, upon request, from Program headquarters in Portland, Oregon. The major improvement of version 2.0 involved the coupling of BWMOD to PROGNOSIS (Crookston 1980 (unpublished), Crookston and Monserud 1981 (unpublished), Crookston et al. 1978). Version 3.0 consists of extensively revised PROGNOSIS and two additional components, BWMOD and BWFLY. All population dynamics from eggs through pupae and the associated biology including host defoliation are simulated in BWMOD. Adult dispersal and egg laying are simulated in BWFLY.

The document contains three major sections. The first describes PROGNOSIS, the tasks it accomplishes, and provides the framework for the second and third sections. The second section describes BWMOD and BWFLY. Data requirements for combined model use are outlined in the third section.

In the following material, where a separate CANUSA-funded research study has or will produce the functional relationships, a list of investigators' names follows an asterisk (*). Those are investigators whose results will provide the information base necessary to generate particular functional forms and parameterize specific equations. As work is completed, we expect to revise or replace existing functions but we will have the components operational to allow review of the interrelationships of component parts as individual studies are complete and data become available for comparisons with model behavior.

PART 1

PROGNOSIS/WESTERN SPRUCE BUDWORM MODEL

PROGNOSIS (Stage 1973) has proved to be a useful tool for comparing different stand treatments (Wykoff et al., in review). The most recent version of PROGNOSIS has been installed and used by several private companies in the United States and Canada. In addition, it is actively used by the Bureau of Land Management, Forest Service Regions 1, 4, and 6, as well as the states of Oregon and Idaho. At this time, PROGNOSIS is being calibrated for eastern Oregon and Washington. Future plans include model calibration for California and Utah as well. Further, PROGNOSIS is currently being incorporated into the AGNET computer network developed for use by land managers.

PROGNOSIS can be used to simulate the effects of:

- Thinning from above and/or below to basal area and/or trees/acre residual densities
- Prescription thinning
- Removal of a specified portion of the diameter distribution.

Through the use of the Regeneration Establishment Extension, the effects of various site preparation methods may be simulated. The addition of the Shrub/Cover Extension provides information relative to game and watershed values. Lastly, other insect models (Douglas-fir tussock moth, mountain pine beetle) may be used to represent management implications which are related to the activities of these species.

The nature of the inland northwest U.S. forests and the complexity of their management led to the following criteria for the design of the model:

- Uses existing inventory methods as sources of input.
- Applies to all timber types and stand conditions encountered in the inventory.
- Treats stands as the unit population.
- Incorporates growth of the current inventory into projections.
- Provides links to other biotic and hydrologic components of the ecosystem.

The model contains explicit components which predict

- Diameter increment
- Height increment
- Change in crown ratio
- Mortality rate

on each of the individual sample trees. The model is an individual tree model which does not contain mapped between-tree spatial relationships. The methodology used in the model, as well as its applicability, are described further in Wykoff et al. (in review).

The relationship between the PROGNOSIS and the BWMOD may be characterized according to the tasks each perform:

- PROGNOSIS estimates growth and yield of a stand of trees in the absence of budworm.
- BWMOD simulates the activities of budworm, the damage done to the foliage, and the subsequent effect on growth.
- PROGNOSIS "controls" BWMOD.

One of the assumptions which was made while developing the PROGNOSIS is that stands of trees grow independently from one another—growth regulating agents in one stand do not affect the simulated development of adjacent stands. Of course, this assumption is invalid when considering budworm or other agents which partially regulate tree growth and move from one stand to another. The inclusion of such agents as predictors of growth in one stand requires that the growth of interdependent stands be simulated in parallel (Crookston and Stage, in prep.).

The following describes the logic involved in the combination of PROGNOSIS and BWMOD (Fig. 1) including the parallel processing of several stands.

==> Do for each stand (loop I)

1. Initialize models; read data and program instructions (SP: Stand Prognosis; BW: Spruce Budworm)
2. Calibrate models
3. Write summary of current inventory
4. Store BW data (in memory)
5. Store stand and tree data (on disk)

==> End loop for stands (loop I)

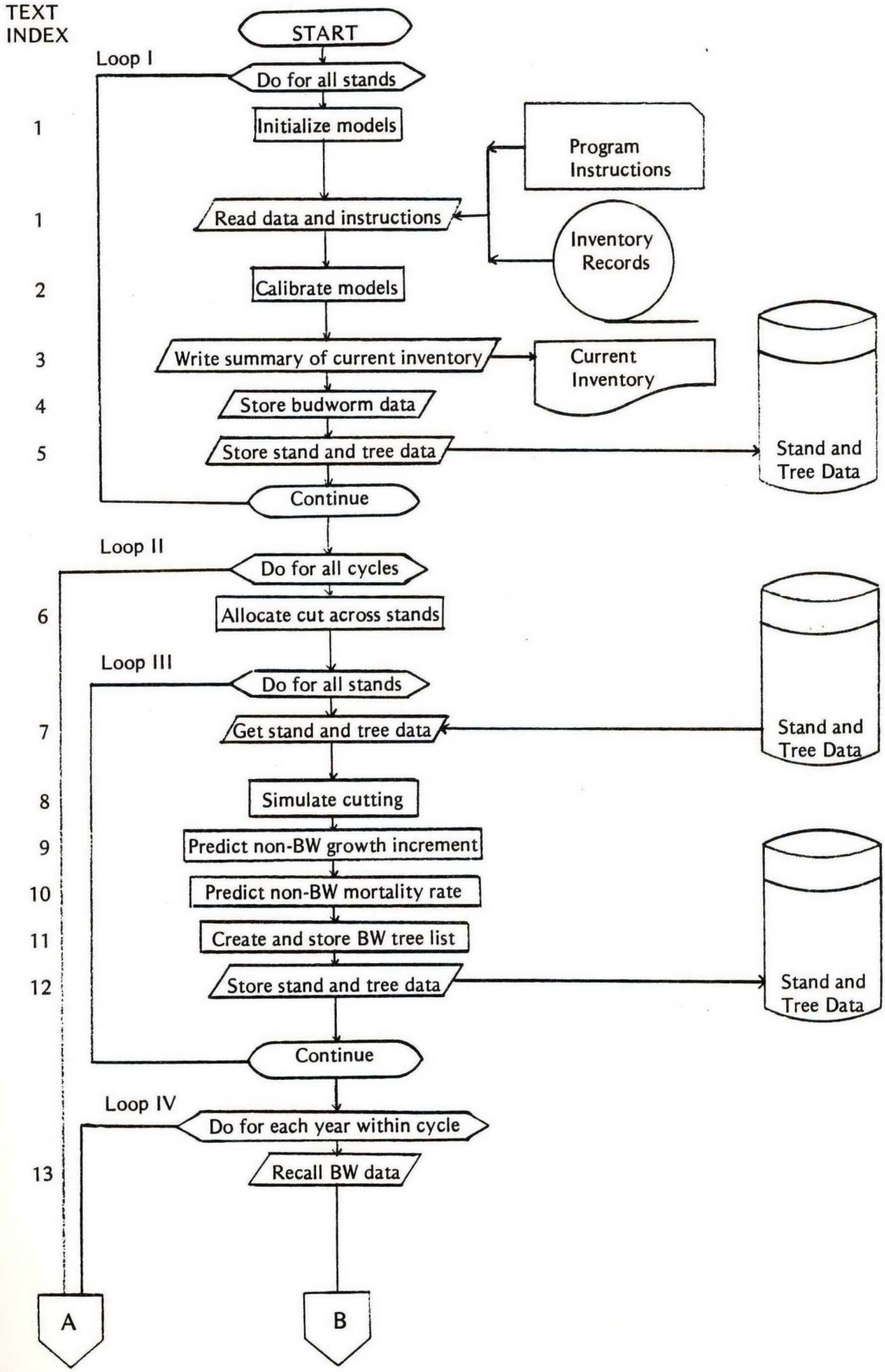
==> Do for all cycles (10 yr standard for tree growth) (loop II)

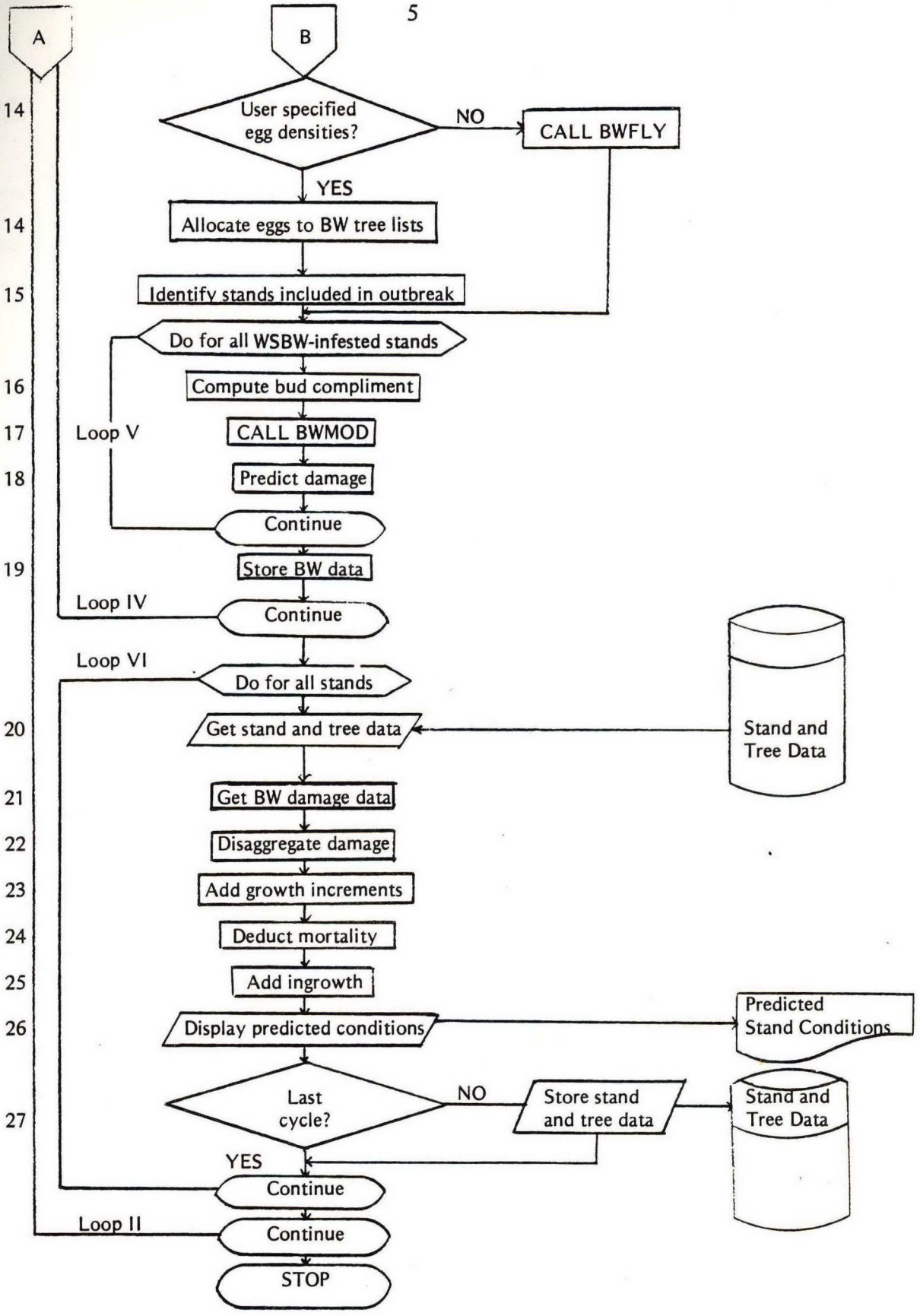
6. Allocate cut across stands

==> Do for all stands (loop III)

7. Get stand and tree data (from disk)
8. Simulate cutting
9. Predict non-BW growth increment
   *Carlson, Ferguson, Foiles, Stage et al.
10. Predict non-BW mortality rates
    *Hamilton, Stage et al.

Figure 1. PROGNOSIS flow diagram showing linkage to BWFLY and BWMOD (from Crookston and Stage, manuscript in preparation).




A
B
14
User specified egg densities?
NO
CALL BWFLY
YES
14
Allocate eggs to BW tree lists
15
Identify stands included in outbreak
Do for all WSBW-infested stands
16
Compute bud compliment
17
Loop V
CALL BWMOD
18
Predict damage
Continue
19
Store BW data
Loop IV
Continue
Loop VI
Do for all stands
20
Get stand and tree data
Stand and Tree Data
21
Get BW damage data
22
Disaggregate damage
23
Add growth increments
24
Deduct mortality
25
Add ingrowth
26
Display predicted conditions
Predicted Stand Conditions
Last cycle?
NO
Store stand and tree data
Stand and Tree Data
27
YES
Continue
Loop II
Continue
STOP

11. Create and store BW tree list including foliage compliment (in memory)
*Burnell, Crookston, Hinckley, Moeur, Scott, Shearer/Tiernan

12. Store stand and tree data (on disk)

= = > End loop for stands (loop III)

= = > Do for each year within cycle (loop IV)

13. Recall BW data (for all stands)

14. Allocate egg masses to BW tree lists

15. Identify stands included in outbreaks
*Heller, Long, Stoszek

= = > Do for all BW-infested stands (loop V)

16. Compute bud compliment
*Burnell, Hinckley, Mouer, Scott, Shearer/Tiernan, Thomson

17. Call BWMOD

18. Predict reductions in radial increment, probability and amount of top kill for BW tree list, and BW-induced mortality.
*Alfaro, Bousfield, Burnell, Carlson, Dewey, Ferguson, Foiles, Scott, Shearer/Tiernan, Thomson, Van Sickle

= = > End loop for BW-infested stands (loop V)

19. Store BW-data

= = > End loop for each year (loop IV)

= = > Do for all stands (loop VI)

20. Get stand and tree data from disk storage

21. Get BW damage data from memory

22. Disaggregate damage
*Alfaro, Burnell, Crookston, Monserud, Scott, Thomson

23. Add growth increments modified according to BW damage

24. Deduct mortality
*Alfaro, Burnell, Scott, Thomson

25. Add ingrowth
*Carlson, Ferguson, Foiles, Shearer/Tiernan

26. Display predicted conditions (print stand table outputs)

27. If not last projection cycle, store stand and tree data on disk.

= = > End loop for all stands (loop VI)

= = > End loop for all cycles (loop II)

28. End simulation

PART 2

OUTLINE OF PROPOSED WESTERN SPRUCE BUDWORM MODELS BWMOD AND BWFLY

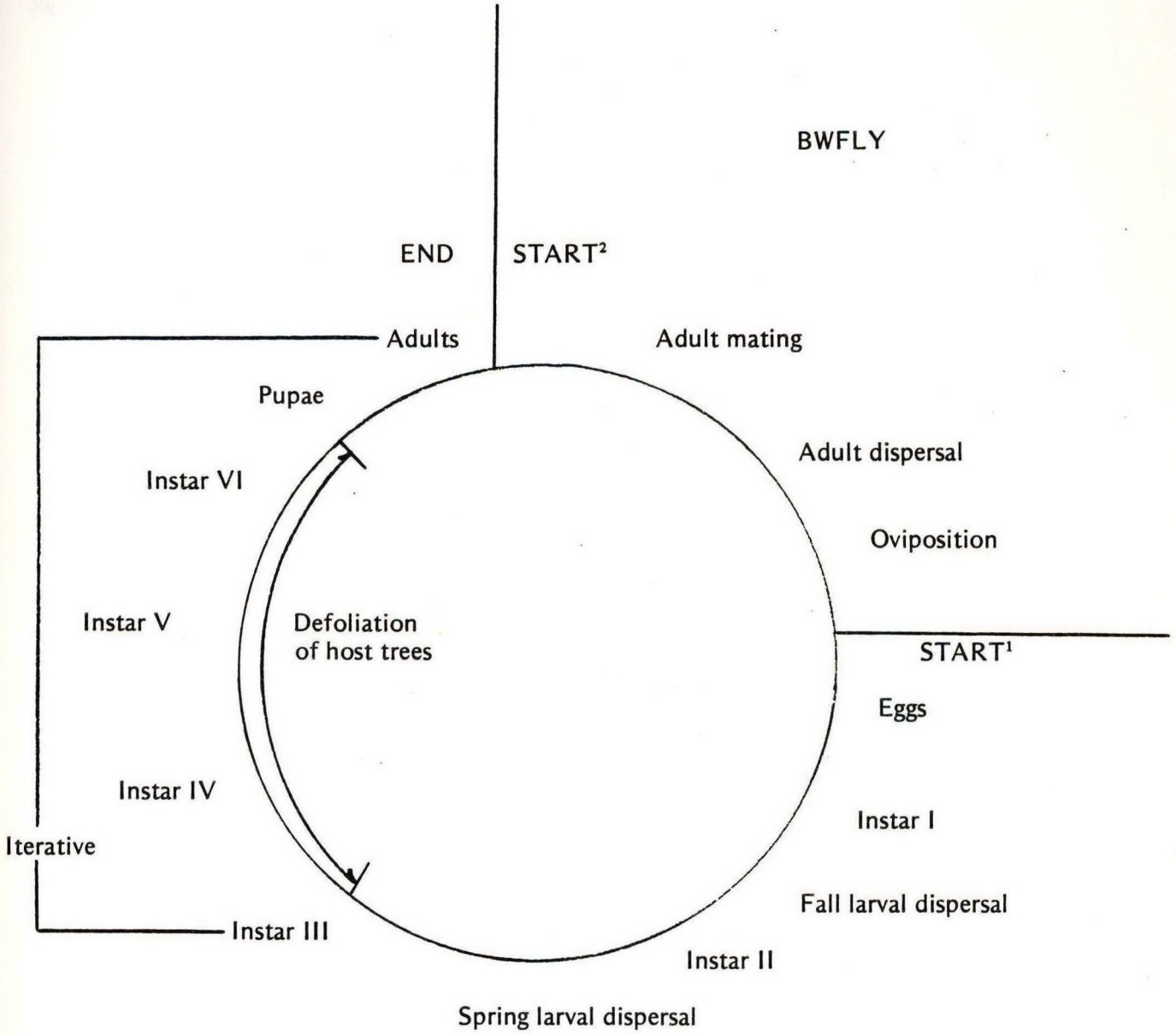
This section contains a description of two models related to western spruce budworm population dynamics and host tree defoliation.

Figure 2 depicts a yearly flow of the system and explains subsections which are controlled by BWFLY (Fig. 3) and BWMOD (Fig. 4). Within each yearly cycle, PROGNOSIS passes foliage to BWFLY and BWMOD in the fall (new growth completed) and bud complement in the spring.

Figure 3 and the related text explain the proposed flow diagram for the BWFLY model. This model contains all spruce budworm adult activities. Its primary function is to disperse adult moths and allocate eggs to foliage. In order to start an outbreak, user specified egg densities are required and BWFLY is bypassed (Fig. 1). From that point on, BWFLY is used each year in a particular stand to distribute eggs generated by the adult population which it receives from BWMOD.

Figure 4 and the associated text explain the proposed outline for BWMOD. This model contains spruce budworm population dynamics from egg densities (which it receives from BWFLY or the user) through adult moth emergence in a given year. In addition, submodels within BWMOD describe interactions between tree host species and the western spruce budworm as they relate to defoliation each year. Within each PROGNOSIS cycle, BWMOD is called once per year for each stand which contains budworm (Fig. 1). Very simply, PROGNOSIS passes BWMOD a foliage matrix, which BWMOD alters depending on densities of the insect and other parameters. BWMOD then returns this changed foliage matrix to PROGNOSIS and updates population levels for use in the adult activities model BWFLY.

Figure 2. General diagram showing yearly western spruce budworm life cycle and related models by event.



START¹ - Entry point if user has specified initial egg densities
START² - Entry point if adults were generated from the previous year

Figure 3. Flow diagram of the proposed model for adult western spruce budworm activities.

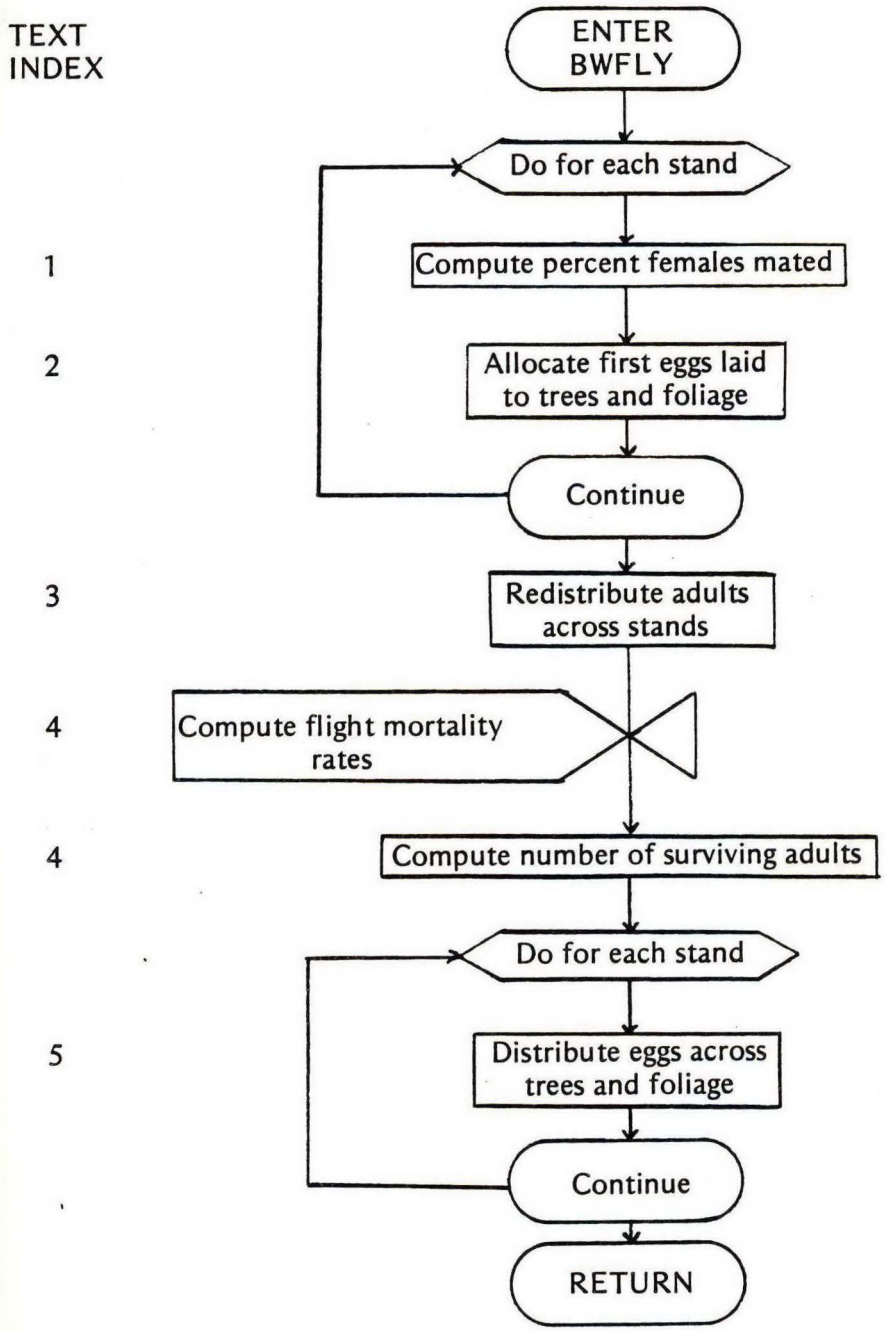
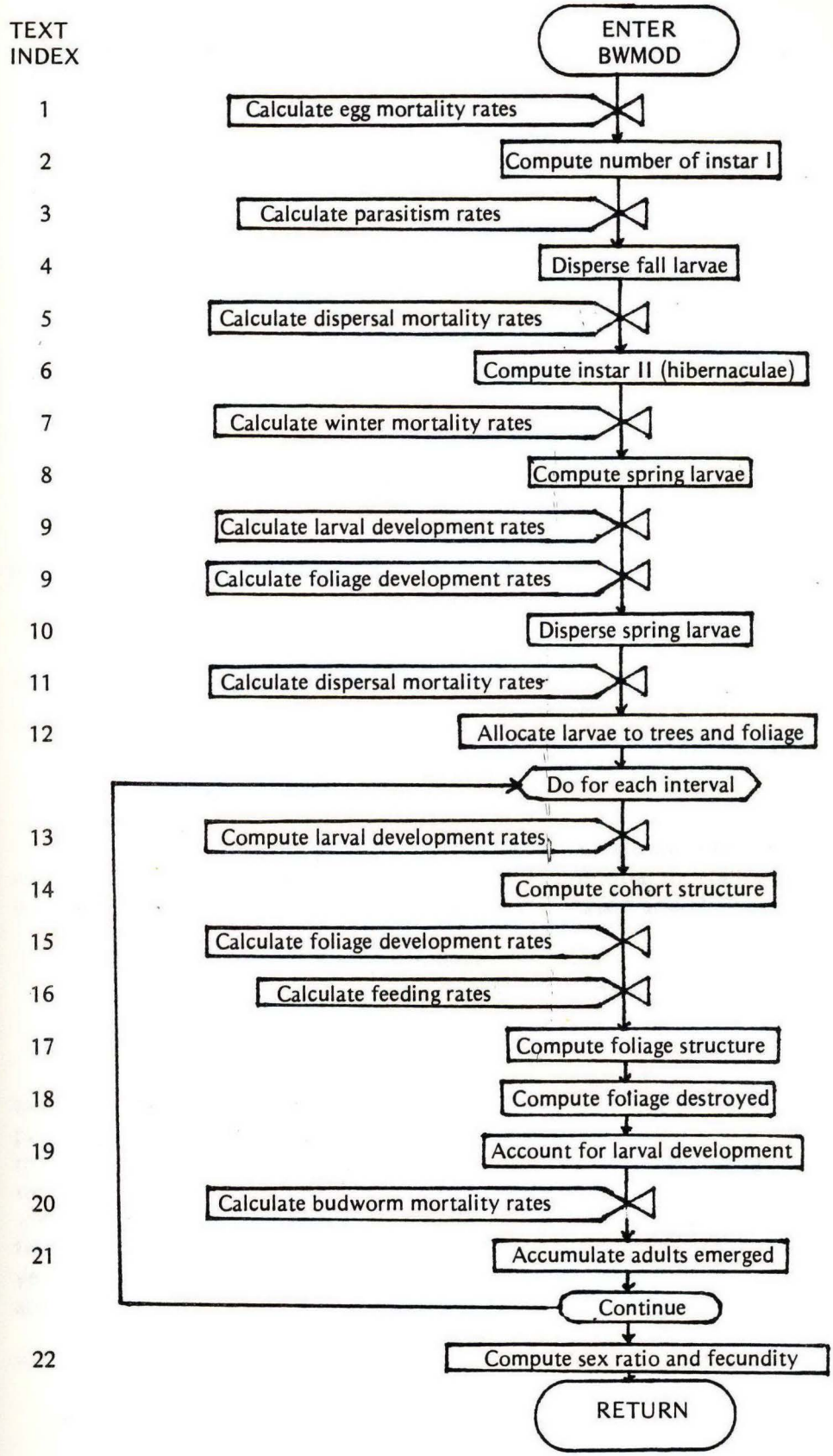


Figure 4. Flow diagram for proposed model of western spruce budworm populations excluding adult dispersal activities.



Outline BWFLY

Adult Activities Loop

Within each PROGNOSIS cycle, BWFLY is called on a yearly basis. Figure 3 shows the 5 major activities which are modeled in BWFLY. Mating success of adult females and allocation of initial egg masses are calculated once for each stand. Adult dispersal, flight mortality rates, and number of surviving adults are all computed once for the matrix of stands which comprise the forest. Finally, the remaining potential eggs are distributed throughtout each stand.

As mentioned earlier, if BWMOD was called during the last year, adult densities are used to generate egg densities (BWFLY), otherwise, egg densities are generated according to user specified conditions which may be either measure of the following:

A. Defoliation history
*Bullard, Wong, Young

B. Enter means and standard deviations for egg levels, specify tree height and species
*Cahill, Campbell/Torgersen, Stipe, Twardus

The following text explains each step of BWFLY as well as notes on existing and expected information inputs. Those steps modeled in BWFLY are:

= = > From PROGNOSIS

= = = > Start loop through stands

1. Compute percent females mated
*Sartwell/Twardus, Shepherd, Waters/Volney
f(budworm density, sex ratio, weather)

Under most conditions, a high percentage of female western spruce budworm moths are mated. However, during this period, there is potential mortality from predators and weather, which could reduce adult numbers (Wellington and Henson 1947, Beaver 1967).

2. Allocate first eggs to trees and foliage
*Beckwith, Campbell/Torgersen, Schmid, Shepherd, Waters/Volney
f(budworm density, defoliation, stand factors, tree height, tree species, weather)

Most of the information on preflight egg mass deposition is related to eastern spruce budworm (Greenbank et al. 1980). However, recent studies on western spruce budworm population dynamics where observed eggs were in some cases twice that expected, suggest that in this species as well, not all deposits are in the stand of origin. Western spruce budworm egg mass size has been found to vary by host tree species and infestation (McKnight 1967, 1969c, 1971, Washburn and Brickell 1973). Densities of egg masses have also been found to be indicative of western budworm population trends and defoliation the following year (Buffam and Carolin 1966, Bullard and Wong 1981, Bullard and Young 1980, Carolin and Coulter 1959, 1972, 1975, McKnight 1967, Silver 1960, Terrell 1961, 1966).

= = = > End loop through stands

3. Redistribute adults across stands
   *Everson/Burnell, Long, McLean, Shepherd, Silversides, Thomson
      f(budworm density, oviposition sites, physical limitations, predators, weather)

A great deal of information exists on dispersal and mortality of eastern spruce budworm adults (Greenbank 1950, 1951, 1956, 1957, 1963a, 1963b, Greenbank et al. 1980, Wellington 1979, Wellington et al. 1950, Wellington and Henson 1947, Wellington and Trimble 1981). Recent studies in the west will generate information on such relationships for western spruce budworm. Predators and weather appear to be important components during this phase.

4. Calculate adult mortality
   *Garton, Long, McLean, Shepherd
      f(budworm density, predators, sex ratio, weather)

Most of the previously published important mortality factors of adult western spruce budworm are contained in literature cited in Item 3 above.

5. Distribute remaining eggs across trees within stands (occurs once for each stand)
   *Beckwith, Campbell/Torgersen, Schmid, Shepherd, Waters/Volney
      f(budworm density, physical limitations, stand factors, tree height, tree species, weather)

See Item 2 above for notes on egg densities.

Outline BWMOD

As with the development of BWFLY, a concurrent literature review was conducted and continues at this time during the formulation of BWMOD. From this review it has become obvious that several authors have developed spruce budworm models with varying degrees of precision. Most models developed at this time are related to eastern spruce budworm dynamics. These include models by Holling et al. 1975, Jones 1976, Kemp et al. 1980, McNamee et al. 1980, Morris 1963, Morris et al. 1958, Thomson 1976, Ung 1979. Of these, only Thomson (1979) and McNamee (1980) deal with population dynamics of western spruce budworm. The former was developed for budworm populations in British Columbia and the latter contains the model which is the subject of this revision.

With the exception of recent studies by CANUSA-West funded investigators, most of the definitive life table work which can be used in modeling has been conducted on the eastern spruce budworm (Miller 1975a, 1957b, 1963, Morris 1963, Morris and Miller 1954). McKnight (1967, 1971), however, has generated life tables for western spruce budworm in Colorado over a two-year period. These studies, though providing valuable information on population changes over time, are often general and do not give a great deal of insight into the individual components which affect life tables in a given year. In the following text, it is assumed these studies touch on all aspects of the model as they relate to budworm and therefore will not be cited repeatedly. Numerous other studies more narrow in scope have been reviewed and will help support the development of particular sections of the model. These studies have not been cited, but are contained in a bibliography in the rear.

The following are the principal steps to be modeled by BWMOD.

==> From PROGNOSIS

1. Calculate egg mortality rates
   *Beckwith, Campbell/Torgersen, Egan, Waters/Volney
   f(egg viability, parasitism, weather)

2. Compute number of instar I budworm (population state variable)
   *Beckwith, Egan, Everson/Burnell, Fellin, Shepherd
   f(weather)

3. Calculate parasitism rates
   *Beckwith, Egan, Everson/Burnell, Fellin, Shepherd, Waters/Volney
   f(budworm density, stand factors, weather)

4. Disperse fall larvae - instar I budworm
   *Burnell/Beckwith, Egan, Everson/Burnell, Fellin, Shepherd, Thomson
   f(budworm density, parasitism, stand factors, weather)

5. Calculate dispersal mortality rates - instar I budworm
   *Burnell/Beckwith, Egan, Everson/Burnell, Fellin
   f(failure to spin, final residence, predators, stand factors, weather)

6. Spin hibernaculae and compute instar II numbers (population state variable)
   *Egan, Everson/Burnell, Fellin, Shepherd
   f(weather)

7. Calculate winter mortality rates - instar II budworm
   *Egan, Fellin, Shepherd
   f(budworm density, weather)

8. Compute spring larvae (population state variable)
   *Egan, Fellin, Shepherd

9. Calculate larval and foliage development rates
   *Burnell, Egan, Everson/Burnell, Fellin, Hinckley, Wagner
   f(weather)

10. Disperse spring larvae - instar II budworm
    *Burnell/Beckwith, Egan, Fellin, Shepherd
    f(budworm density, stand factors, parasitism, weather)

11. Calculate dispersal mortality rates - instar II budworm
    *Burnell/Beckwith, Egan, Everson/Burnell, Fellin
    f(final residence, stand factors, predators, weather)

12. Allocate larvae to trees and foliage - instar II budworm
    *Burnell/Beckwith, Schmid, Shearer/Tiernan, Stevens, Wagner, Waters/Volney

    A. Old needles
       f(budworm density, supply of new, supply of swollen buds, tree species, weather)

    B. New needles
       f(budworm density, preference, supply of new, tree species, weather)

    C. Swollen buds
       f(budworm density, preference, supply of buds, tree species, weather)

    D. Flowers and cones
       f(budworm density, preference, supply of flowers and cones, tree species, weather)

===> Start feeding loop

13. Calculate budworm development rates - instar III to adult
    *Beckwith, Brewer/Capinera/Logan, Cates, Everson/Burnell, Shepherd, Thomson, Wagner, Waters/Volney
    f(budworm density, foliage available, foliage quality, weather)

14. Compute budworm cohort structure - instar III to adult (population state variable)
    *Beckwith, Campbell/Torgersen, Shepherd, Wagner
    f(parasitism, predation, weather)

15. Calculate foliage development rates
    *Cates, Everson/Burnell, Hinckley, Shepherd, Wagner
    f(moisture stress, tree species, weather)

16. Calculate feeding rates
    *Brewer/Capinera/Logan, Hinckley, Shepherd, Wagner
    f(cohort structure, foliage quality, foliage quantity, tree species, weather)

17. Compute foliage structure (foliage state variable)
    *Brewer/Capinera/Logan, Burnell, Cates, Everson/Burnell, Hinckley
    f(foliage quality, tree species, weather)

18. Compute foliage destroyed
    *Brewer/Capinera/Logan, Cates, Everson/Burnell, Shearer/Tiernan, Wagner

A. Old needles
f(cohort structure, foliage quality, tree species, weather)

B. New needles
f(cohort structure, foliage quality, tree species, weather)

C. Swollen buds
f(cohort structure, foliage quality, tree species, weather)

D. Flowers and cones
f(cohort structure, tree species, weather)

19. Account for larval development
*Beckwith, Brewer/Capinera/Logan, Cates, Wagner
f(foliage consumption, foliage quality, parasitism, tree species, weather)

20. Calculate budworm mortality rates
*Beckwith, Campbell/Torgersen, Garton, Robertson/Berry, Schmid, Waters/Volney
f(budworm density, direct control efforts, starvation, tree species, weather)

21. Accumulate number of adults emerged (population state variable)
*Beckwith, Campbell/Torgersen, Garton, Robinson/Berry, Schmid, Shepherd, Waters/Volney
f(budworm density, parasites, predators, tree species, weather)

= = = > End feeding loop

22. Compute sex ratio and fecundity
*Beckwith, Brewer/Capinera/Logan, Campbell/Torgersen, Cates, Fellin, Shepherd

= = > Return to PROGNOSIS

PART 3

DATA REQUIRED TO USE THE COMBINED PROGNOSIS/WSBW MODEL

Within this section, four data items are identified. Items 1, 2, and 4 are data required for running of PROGNOSIS. Methods for sampling variables outlined by these items are reasonably standardized throughout the region where PROGNOSIS is being used. Item 3, however, represents additional data required to run the BWMOD/BWFLY extension. Methods for estimating these variables have in the past been somewhat variable, and this would introduce bias into the simulation. However, efforts are being made to standardize sampling procedures. This should help improve the reliability of these input variables and resulting simulations.

1. Inventory design used to measure the stand

    A. Basal area factor for variable radius points

    B. Fixed plot area (indicate units)

    C. Critical diameter (inches), if fixed plots are used to measure small trees and variable radius points are used to measure large trees

2. Site conditions

    A. Slope (percent)

    B. Aspect (code 1 = north; 2 = northeast, . . ., 8 = northwest; 9 = level)

    C. Elevation (hundreds feet)

    D. Habitat type, community type, site class, or site index (indicate units)

    E. Location (nearest National Forest)

3. WSBW population levels, using one or both of the following methods:

    A. Defoliation rating by tree species

        i. Current growth

        ii. Total foliage biomass

    B. Mean and standard deviation of WSBW population samples by tree species

        i. Egg mass

        ii. Larval

        iii. Pupal samples

4. Characteristics of each tree measured in the inventory

   A. Variables that must be measured on all trees

      i. Identification of plot on which the tree was measured (a blank field may be used)

      ii. Tree species

      iii. Current dbh (inches)

      iv. Number of trees represented by the record (a blank field indicates 1 tree is represented)

   B. Variables that may be sub-sampled or omitted

      i. Periodic diameter growth (inches)

      ii. Crown ratio (should measure on all trees. Can be replaced by crown length)

      iii. Total tree height (feet)

      iv. Periodic height growth (trees less than about 3" dbh)

      v. Tree value class (1 = preferred, 2 = excess, 3 = cull tree)

   C. Additional variables which improve the accuracy of the projection

      i. Tree history (codes are: 5 = recent mortality (indicate how many years ago the tree must have died to be included as recent mortality, and be consistent for the stand); 6 or 7 = old mortality; 9 = tree record is automatically skipped, other codes indicate that the tree is alive

      ii. Height to topkill

      iii. Damage code (codes are: 73 = top is dead, 74 = top is missing, 0 or other codes are not used and indicates no damage)

      iv. Marking codes (0 or 1 = leave tree, 2 or greater = cut tree (used to simulate prescription thinning))

BIBLIOGRAPHY

Batzer, H.O.
1968. Hibernating site and dispersal of spruce budworm larvae as related to damage of sapling balsam fir. J. Econ. Entomol. 6:212-220.

Bean, J.L.
1961a. Predicting emergence of second instar spruce budworm larvae from hibernation under field conditions in Minnesota. Ann. Ent. Soc. Am. 54:175-177.

Bean, J.L.
1961b. The use of balsam fir shoot elongation for timing spruce budworm aerial spray programs in the lake states. J. Econ. Entomol. 54:996-1000.

Bean, J.L. and L.F. Wilson.
1964. Comparing various methods of predicting development of the spruce budworm, *Choristoneura fumiferana,* in northern Minnesota. J. Econ. Entomol. 57:925-927.

Beaver, D.L.
1967. Feeding niches of flycatchers in a montane forest in Colorado. M.S. Thesis. Colo. State Univ. 122 p.

Beckwith, R.C.
1981. Effects of constant laboratory temperatures on the Douglas-fir tussock moth (manuscript). Pac. Northwest Range and Exp. Sta. 21 p.

Blais, J.R.
1948. The spruce budworm in relation to flowering condition of the host tree. Can. For. Serv. Sci. Serv. Div. Ent. For. Ins. Invest. Bi-Mon. Prog. Rep. 4(5):1.

Blais, J.R.
1957. Spruce budworm development in the Gaspe' Peninsula. Can. For. Serv. Sci. Serv. Ent. For. Ins. Invest. Bi-Mon. Prog. Rep. 13(1):1-2.

Blais, J.R.
1968. Regional variation in susceptibility of eastern North American forests to budworm attack based on the history of outbreaks. Forestry Chron. 44:17-23.

Bray, J.R.
1965. Forest growth and glacial chronology in northwest North America in relation to solar activity. Nature 205:440-443.

Bruhn, J.A.
1980. A stochastic model for simulation of daily weather. Prot. Ecol. 2:199-208.

Buffam, P.E. and V.M. Carolin, Jr.
1966. Determining trends in budworm egg populations. J. Econ. Entomol. 56:1442-1444.

Bullard, A.T. and J. Wong.
1981. Evaluation of multiple regression models for prediction of western spruce budworm defoliation on Douglas-fir. USDA For. Serv. Forest Pest Management Methods Application Group Rep. No. 81-1. 25 p.

Bullard, A.T. and R.W. Young.
1980. Prediction of western spruce budworm defoliation on Douglas-fir. USDA For. Serv. Forest Pest Management Methods Application Group Rep. No. 80-10. 25 p.

Cameron, D.G., G.A. McDougall, and C.W. Bennett.
1968. Relation of spruce budworm development and balsam fir shoot growth to heat units. J. Econ. Entomol. 61:857-858.

Campbell, J.B., and K.E. Smith.
1980. Climatological forecasts for southern pine beetle infestations. Southern Geog. 20:16-30.

Campbell, R.E.
1972. Prediction of air temperature at a remote site from official station weather records. USDA For. Serv. Rocky Mtn. For. Range and Exp. Sta. Res. Note RM-223. 4 p.

Campbell, R.K.
1974. Use of phenology for examining provenance transfers in reforestation of Douglas-fir. J. of Applied Ecology. 11(3):1069-1080.

Campbell, R.K. and A.I. Sugano.
1975. Phenology of bud burst in Douglas-fir related to provenance, photoperiod, chilling and flushing temperature. Bot Gaz. 136:290-298.

Campbell, R.K. and A.I. Sugano.
1979. Genecology of bud-burst phenology in Douglas-fir: Response to flushing temperature and chilling. Bot. Gaz. 140:223-231.

Carolin, V.M., Jr., and W.K. Coulter.
1959. Research findings relative to the biological evaluation of the spruce budworm infestations in Oregon. USDA For. Serv. Pac. Northwest For. and Range Exp. Sta. 39 p.

Carolin, V.M. and W.K. Coulter.
1972. Sampling populations of western spruce budworm and predicting defoliation on Douglas-fir in eastern Oregon. USDA For. Serv. Res. Pap. PNW-149. 38 p.

Carolin, V.M. and W.K. Coulter.
1975. Comparison of western spruce budworm populations and damage on grand fir and Douglas-fir trees. USDA For. Serv. Res. Pap. PNW-195. 16 p.

Cook, W.C.
1924. Climate variations and moth flight at Bozeman, Mt. Can. Entomol. 56:229-234.

Cook, W.C.
1929. A bioclimatic zonation for studying the economic distribution of injurious insects. Ecology 10:282-293.

Crookston, N.L.
1980. Interface between the stand prognosis model and western spruce budworm model—Version 2.0 (unpublished). 39 p.

Crookston, N.L., R.C. Roelke, D.G. Burnell, and A.R. Stage.
1978. Evaluation of management alternatives for lodgepole pine stands. P. 114-122 *in* Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests. Symposium Proceedings. University of Idaho. 224 p.

Crookston, N.L. and A.R. Stage.
Parallel processing in the prognosis model (in preparation).

Gill, D.E.
1978. On selection at high population density. Ecology 56:1289-1291.

Greenbank, D.O.
1950. Spruce budworm moth flight on Green River watershed. Dominion [Can.] Dep. Agr. Sci. Serv. Div. Entomol. Forest. Ins. Invest. Bi-Mon. Prog. Rep. 6(1):1.

Greenbank, D.O.
1951. Spruce budworm moth population studies. Can. Dep. Agr. Sci. Serv. Div. Forest Biol. Bi-Mon. Prog. Rep. 7(6):1.

Greenbank, D.O.
1956. The role of climate and dispersal in the initiation of outbreaks of the spruce budworm in New Brunswick. I. Role of climate. Can. J. Zool. 34:453-476.

Greenbank, D.O.
1957. The role of climate and dispersal in the initiation of outbreaks of the spruce budworm in New Brunswick. II. The role of dispersal. Can. J. Zool. 35:385-403.

Greenbank, D.O.
1963a. The analysis of moth survival and dispersal in the unsprayed area. P. 87-89 *in* Morris, R.F. (ed.). The Dynamics of Epidemic Spruce Budworm Populations. Entomol. Soc. Can. Mem. 31. 332 p.

Greenbank, D.O.
1963b. Climate and the spruce budworm. P. 174-180 *in* Morris, R.F. The Dynamics of Epidemic Spruce Budworm Populations. Entomol. Soc. Can. Mem. 31. 332 p.

Greenbank, D.O.
1970. Climate and the ecology of the balsam wooly aphid. Can. Ent. 102:546-578.

Greenbank, D.O., G.W. Schaefer, and R.C. Rainey.
1980. Spruce budworm (Lepidoptera: Tortricidae) moth flight and dispersal: New understanding from canopy observations, radar and aircraft. Mem. Ent. Soc. Can. No. 110. 49 p.

Hard, J., S. Tunnock, and R. Eder.
1980. Western spruce budworm defoliation trend relative to weather in the northern region, 1969-1979. USDA For. Serv. State and Private Forestry Rep. No. 80-4. 26 p.

Hardman, J.M.
1976. Deterministic and stochastic models simulating the growth of insect populations over a range of temperatures under Malthusian conditions. Can. Ent. 108: 907-924.

Harris, J.W.E.
1963. Sampling the egg stages of the two-year-cycle spruce budworm near Babine Lake, B.C. Forestry Chron. 39:199-204.

Hauf, W.O.
1966. The significance of biometerology in the ecology of insects. J. Biometerol. 10:241-252.

Haupt, H.F.
1979. Local climatic and hydrologic consequences of creating openings in climax timber of north Idaho. USDA For. Serv. Res. Pap. INT-223. 43 p.

Holling, C.S., G.B. Dantzig, G. Baskerville, D.D. Jones, and W.C. Clark.
1975. A case study of forest ecosystem/pest management. Proceedings Int. Can. Conf. on Applied Systems Analysis.

Ives, W.G.H.
1974. Weather and outbreaks of the spruce budworm, *Choristoneura fumiferana.* Northern For. Res. Cen., Edmonton, Alberta. Inf. Rep. NOR-X-118. 28 p.

Johnson, P.C. and R.E. Denton.
1975. Outbreaks of the western spruce budworm in the American northern Rocky Mountain area from 1922 through 1971. USDA For. Serv. Gen. Tech. Rep. INT-20. 144 p.

Jones, D.D.
1976. Budworm site model. Working paper W-13. Institute of Res. Ecology. Univ. of B.C., Vancouver. 66 p.

Kemp, W.P., J.P. Nyrop, and G.A. Simmons.
1980. Simulation of the effects of stand factors on spruce budworm (Lepidoptera: Tortricidae) larval redistribution. Great Lakes Entomol. 13:81-91.

Lindsey, A.A., and J.E. Newman.
1956. Use of official weather data in spring time temperature analysis of an Indiana phenological record. Ecology 37:812-823.

Lowry, W.P.
1966. Apparent meterological requirements for abundant cone crops in Douglas-fir. Forest Sci. 12:185-192.

Mason, C.J. and M.L. McManus.
1980. The role of dispersal in the natural spread of the gypsy moth. P. 94-115 *in* Berryman, A.A., and L. Safranyik (eds.). Dispersal of Forest Insects. Proceedings of the Second IUFRO Conf. Sandpoint, Idaho, 1979. 278 p.

McKnight, M.E.
1967. Ecology of the western spruce budworm, *Choristoneura occidentalis* Freeman (Lepidoptera:Tortricidae) in Colorado. Ph.D. thesis. Colo. State Univ. 206 p.

McKnight, M.E.
1969a. Estimating defoliation of Douglas-fir and white fir by the western spruce budworm. USDA For. Serv. Rocky Mtn. For. and Range Exp. Sta. Res. Note RM-144. 3 p.

McKnight, M.E.
1969b. Distribution of hibernating larvae of the western budworm, *Choristoneura occidentalis,* on Douglas-fir in Colorado. J. Econ. Entomol. 62:139-142.

McKnight, M.E.
1969c. Estimating numbers of eggs in western budworm egg masses. USDA For. Serv. Rocky Mtn. For. Range and Exp. Sta. Res. Note RM-146. 4 p.

McKnight, M.E.
1971. The natural mortality of the western spruce budworm, *Choristoneura occidentalis*, in Colorado. USDA For. Serv. Res. Pap. RM-81. 12 p.

McNamee, P.J.
1979. A process model for the eastern blackheaded budworm (Lepidoptera:Tortricidae). Can. Ent. 111:55-66.

McNamee, P.J.
1980. Update to simulation modelling workshop on western spruce budworm population dynamics (unpublished). 5 p.

McNamee, P.J., R. Everitt, N. Sonntag, and M. Staley.
1980. Simulation modelling workshop on western spruce budworm population dynamics (January 28 - February 1, 1981). CANUSA-USDA For. Serv. Pac. Northwest For. and Range Exp. Sta. Misc. Rept. 120 p.

Miller, C.A.
1957. A technique for estimating the fecundity of natural populations of the spruce budworm. Can. J. Zool. 35:1-13.

Miller, C.A.
1958. The measurement of spruce budworm populations and mortality during the first and second instars. Can. J. of Zool. 36:409-422.

Miller, C.A.
1963. The bionomics of the spruce budworm. P. 12-19 *in* Morris, R.F. (ed.). The Dynamics of Epidemic Spruce Budworm Populations. Mem. of the Ent. Soc. of Can. No. 31. 332 p.

Miller, C.A., D.C. Eidt, and G.A. McDougall.
1972. Predicting spruce budworm development. Dep. Env. Can. For. Serv., Bi-Mon. Res. Notes 27:33-34.

Miller, C.A. and T.R. Renault.
1976. Incidence of parasitoids attacking endemic spruce budworm (Lepidoptera: Tortricidae) populations in New Brunswick. Can. Ent. 108:1045-1052.

Monserud, R.A.
1980. Implementation of prognosis model for forest stand development for combined assessment of silvicultural Douglas-fir tussock moth control activities: Final report to Douglas-fir Tussock Moth Program. USDA For. Serv. Int. For. and Range Exp. Sta. INT- . 90 p.

Monserud, R.A., and N.L. Crookston.
1981. A user's guide to the combined stand prognosis and Douglas-fir tussock moth outbreak model. USDA For. Serv. Int. For. and Range Exp. Sta. INT- . 110 p.

Morris, R.F., W.F. Cheshire, C.A. Miller, and D.G. Mott.
1958. The numerical response of avian and mammalian predators during a gradation of the spruce budworm. Ecology 39:487-494.

Morris, R.F. and C.A. Miller.
1954. The development of life tables for the spruce budworm. Can. J. of Zool. 32:283-301.

Morris, R.F. and D.G. Mott.
1963. Dispersal and the spruce budworm. P. 180-189 *in* Morris, R.F. (ed.). The Dynamics of Epidemic Spruce Budworm Populations. Mem. of the Ent. Soc. of Can. No. 31. 332 p.

Morris, R.F., F.E. Webb, and C.W. Bennett.
1956. A method of phenological survey for use in forest insect studies. Can. J. Zool. 34:533-540.

Morris, W.G., R.R. Silen, and H. Irgens-Moller.
1957. Consistency of bud bursting in Douglas-fir. J. of Forestry. 55:208-210.

Richardson, C.W.
1981. Stochastic simulation of daily precipitation, temperature, and solar radiation. Water Resources Res. 17:182-190.

Shaw, J.G. and C.H.A. Little.
1973. Dispersal of second instar spruce budworm. Dep. Env. Can. For. Serv., Shaw, . Res. Notes 29:30-31.

Shaw, J.G. and C.H.A. Little.
1976. Natural variation in balsam fir foliar components of dietary importance to the spruce budworm. Can. J. For. Res. 7:47-53.

Shelford, V.E.
1926. The relation of the abundance of parasites to weather conditions. J. Econ. Entomol. 19:283-289.

Silver, G.T.
1960. Notes on a spruce budworm infestation in British Columbia. Forestry Chron. 36:362-374.

Stage, A.R.
1973. Prognosis model for stand development. USDA For. Serv. Res. Pap. INT-137. 31 p.

Stage, A.R. and D.G. Burnell.
Data collection procedures for whole-tree sampling of foliage affected by insect defoliation (unpublished). 12 p.

Stage, A.R. and D.E. Ferguson.
1981. Regeneration modelling as a component of forest succession simulation. Proc. 1981 Northwest Scientific Assoc. Meeting, Symp. on Forest Succession Meeting, Symp. on Forest Succession Modelling (in press), Oregon State Univ., Corvallis, OR.

Terrell, T.T.
1961. Techniques of spruce budworm surveys in the northern Rocky Mtn. region 1960. Progress Rep. USDA For. Serv. Int. For. and Range Exp. Sta. Mimeo. 14 p.

Terrell, T.T.
1966. Spruce budworm survey methods in the northern region. Coop. Econ. Insect. Rep. 16:1071-1072.

Thomson, A.J.
1979. Evaluation of key biological relationships of the western budworm and its host trees. Dep. Env. Can. Pac. For. Res. Cen. Rep. No. BC-X-186. 19 p.

Tunnock, S.
1974. Western spruce budworm egg masses for predicting defoliation potential in the northern region. Progress Rep. USDA For. Serv. Northern Reg. State and Private For., Missoula, MT. 10 p.

Twardus, D.B.
1980. Evaluation of weather patterns in relation to western spruce budworm outbreaks in north-central Washington, 1970-1980. USDA For. Serv. FIDM Pac. Northwest Region Misc. Rep. 16 p.

Ung, C.H.
1979. A dynamic programming approach for optimizing logging and spraying against spruce budworm. Interim Rep. CANUSA Working Group meetings. 19 p.

Wagg, J.W.B.
1958. Environmental factors affecting spruce budworm growth. Res. Bull. Oregon St. Forestry 11:1-27.

Walters, C.J., and R.M. Peterman.
1974. A systems approach to the dynamics of spruce budworm in New Brunswick. Quaes. Entomol. 10:177-186.

Washburn, R.I. and J.E. Brickell.
1973. Western spruce budworm egg mass dimensions—An influence on population estimates. USDA For. Serv. Res. Pap. INT-138. 20 p.

Wellington, W.G.
1948. The light reactions of the spruce budworm *Choristoneura fumiferana* (Lepidoptera:Tortricidae). Can. Entomol. 80:56-82.

Wellington, W.G.
1954. Weather and climate in forest entomology. P. 11-18 *in* Sargent, F., II, and R.G. Stone. Recent Studies in Bioclimatology. Meterological Mono. Vol. 2.

Wellington, W.G.
1965. The use of cloud patterns to outline areas with different climates during population studies. Can. Ent. 97:617-631.

Wellington, W.G.
1980. Dispersal and population change. P. 11-24 *in* Berryman, A.A., and L. Safranyik (eds.). Dispersal of Forest Insects. Proc. of the Second IUFRO Conf., Sandpoint, ID, 1979. 278 p.

Wellington, W.B., J.J. Fettes, K.B. Turner, and R.M. Belyea.
1950. Physical and biological indicators of the development of outbreaks of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera:Tortricidae). Can. J. Res. Sec. D. 28:308-331.

Wellington, W.G. and W.R. Henson.
1947. Notes on the effects of physical factors on the spruce budworm (*Choristoneura fumiferana* (Clem.)). Can. Entomol. 79:168-170.

Wellington, W.G. and R.M. Trumble.
1981. Weather. *In* Huffaker, C.B. and R.L. Rabb (eds.). Ecological Entomology (in preparation).

Willhite, E.A.
1979. Genetics of outbreaking western spruce budworm *Choristoneura occidentalis* Freeman (Lepidoptera:Tortricidae) populations in northern Idaho and Montana. Masters thesis. Univ. of Idaho. Moscow, ID. 106 p.

Wykoff, W.R., N.L. Crookston, and A.R. Stage.
Users' guide to the stand prognosis model. USDA For. Serv. Gen. Tech. Rep. INT 210 p.